

The Distribution and Classification of the Onychophora.

By

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With 13 Figures.

THE genus *Peripatus*, so far as adult conformation is concerned, is a very homogeneous one. It was pointed out by me in 1888 that the species from the same part of the world resembled each other more closely than they do species from other regions, and that the species in this way fall into discontinuous groups which were defined in the monograph then published. Since the publication of that monograph, specimens have been recorded from two other regions, viz. New Britain and Equatorial Africa, and the species established on these specimens completely conform to the above generalisation. So that now there are six discontinuous groups of species of *Peripatus* all capable of precise definition. They are (1) the South African group; (2) the Australasian group; (3) the *Peripatus* from New Britain; (4) those from the Neotropical Region; (5) the *Peripatus* from the Congo; and (6) the four species from Malaya. To these must be added a seventh group formed by the Chilean *Peripatus*, *P. blainvillei*, which, as Bouvier has shown, is quite distinct from the other neotropical species, and from all the species found in other regions. The remarkable point about these groups is that they are sharply marked off from one another, and, though there is the usual interdigitation of char-

acters, there is not the slightest difficulty in assigning all of the known species to their groups. When, in 1888, I recognised the existence of this grouping, I carefully considered the desirability of establishing them as distinct genera or subgenera, but I came to the conclusion that it would be rash to do so, partly because it was by no means certain that they would stand the test of later discoveries, and partly because the known species were so small in number and so easy to handle from a classificatory point of view, that there did not appear to be any advantage to be gained by so doing.

It is now twenty years since the publication of my monograph, and it is of interest to inquire to what extent later discoveries have confirmed or disproved the conclusions I then came to. The present is a particularly appropriate time for doing this, on account of the recent publication of Professor Bouvier's fine monograph on the genus. In this important work M. Bouvier has accurately recorded the characters of a considerable number of new species; he has defined with precision some species of which very little, sometimes nothing, was known; he has added greatly to our knowledge of the anatomy of the genus; and lastly, he has established the existence of two new primary localities for the group. By primary localities I mean localities in which all the species possess a set of characters which differentiate them from any of the groups of species previously recognised. These are the Congo and Chili. It is true that Bouvier associates these two newly defined species with certain of the older groups; he associates the Congo *Peripatus* with the Neotropical group, and the Chilian species with a section of the South African, but I do not agree with him in this, and it is the object of this paper to inquire (1) whether he is justified in making this association, and (2) whether the creation of genera and the association of them into families and subfamilies is in the interest of zoological science at the present time. Before doing this I may briefly recall the other important systematic work which has been done on the genus since 1888. In 1898 Willey described a new species which

he discovered in New Britain, and he showed that it possesses characters peculiar to itself which sharply differentiate it from all other known species. In 1901 Evans described three new species which he had found in the Malay Peninsula, and he showed that they possessed some peculiar features which are also presented by the Sumatran species, and are not found in any of the other known species. He thus established the reality of the Sumatran species, which I had been obliged to leave doubtful, and definitely established a new group of species from the Malayan Region distinct from the species of the other great geographical groups.

Purcell (1899) made a thorough and most valuable revision of the South African species, and discovered that one of them differs from the rest in points which seemed to justify the creation of a special genus *Opisthopatus* for its reception. In addition to this work, important observations were made upon the Australasian species by Fletcher and by Dendy, the last of whom discovered that some of the species from this region are normally oviparous; by Miss Sheldon on the development of a New Zealand species; by Sclater on the development of a Neotropical species; by Willey and Evans on the development of the New Britain and Malayan species respectively. With this work, however, I am not so much concerned here, excepting in so far as it adds to our knowledge of the remarkable variety in the structure of the ovum and early development in the genus.

In 1894 Pocock¹ definitely exalted three of my specific groups to generic rank, and named them: *Peripatus* (the American species), *Peripatopsis* (the South African), and *Peripatoides* (the Australasian). This example was followed, and the result is that we now have not only seven genera, viz. *Peripatus*, *Peripatopsis*, *Peripatoides*, *Paraperipatus* (Melanesia), *Eoperipatus* (Malaya), *Ooperipatus* (Australasia), *Opisthopatus* (South Africa),

¹ R. J. Pocock, "Contribution to our Knowledge of the Arthropod Fauna of the West Indies: II. Malacopoda or Prototracheata," 'Journ. Linn. Soc.' (Zool.), xxiv, 1894, p. 518.

and possibly *Mesoperipatus* (Congo), but long discussions as to which of them are valid and how they should be grouped in families and subfamilies. It has led, in other words, to hair-splitting and prolixity. But it has done more than this: it has led one investigator, who, by his admirable work, had definitely established the existence of a group of species (the Malayan) which I had left doubtful, to assert that my grouping of the species has "no foundation in fact," and that it had been "effectually disposed of"; and it has led workers at our genus to ignore the real problem at issue, and to substitute for it meaningless discussions as to the primitiveness of characters and phylogenetic derivation of species.

Now all this, and the very inappropriate names which have been given to some of the genera, would have been avoided if a little patience had been exercised and we had been allowed to await what future work would bring. To ascertain that we need only turn to the important facts which have been collected by the recent admirable workers in the subject—to the memoirs of Willey, Purcell, Evans, and Bouvier. These observers have clearly shown, though some of them would be far from admitting it, that the geographical grouping of the species is a perfectly sound one, and that no subordination of these into families or subfamilies is, in the present state of knowledge, either admissible or desirable. Whether it is desirable to coin generic names for these groups seems to me a matter of small importance. The important point is to recognise the fact that they exist, and to make the utmost possible use of it in our attempts to solve the great problem of species.

Personally I think it premature, unnecessary, and inconvenient to establish genera at the present moment. At the same time, it is convenient to designate each of the seven groups by a name which definitely connects it with the locality. The names which I venture to suggest are shown in the following list:

- (1) The species of the neotropical region except Chili—
Neo-Peripatus.
- (2) The species from tropical Africa—**Congo-Peripatus.**
- (3) " " Malaya—**Eo-Peripatus.**
- (4) " " South Africa—**Capo-Peripatus.**
- (5) " " New Britain—**Melano-Peripatus.**
- (6) " " Australasia—**Austro-Peripatus.**
- (7) " " Chili—**Chilio-Peripatus.**

I shall now attempt to show that the species of each of these groups are distinct from those of the others, and that if generic names are to be given, they must follow the lines of geographical cleavage. M. Bouvier does not accept them all. He associates Congo-Peripatus with Neo-Peripatus, and Chilio-Peripatus with that section of Capo-Peripatus, to which Purcell has given the generic name of *Opisthopatus*. But, as I shall endeavour to show in the sequel, the genus *Opisthopatus* cannot be maintained, and the Congo-Peripatus and Chilio-Peripatus are as distinct as any of the other groups.

I will begin by examining each group in detail, both from a morphological and distributional point of view, and then we shall be in a position to institute a detailed comparison between them.

NEO-PERIPATUS.—*Peripatus* is generally distributed in the neotropical region from Rio de Janiero in the south to Mexico in the north, and it is found in many of the West Indian Islands. West of the Andes its southern limit appears to be Bolivia. All the species in this area belong to the group Neo-Peripatus. A single species (*P. blainvillei*) is known from Chili (Chiloe and near Villa Rica), but this Bouvier has shown to belong to a distinct type. The characters of Neo-Peripatus, of which twenty-nine species are known, are as follows:

1. The number of legs (twenty-three to forty-three pairs) is variable in the same species.

2. Inner jaw with a diastema and a saw of denticles (Fig. 1).

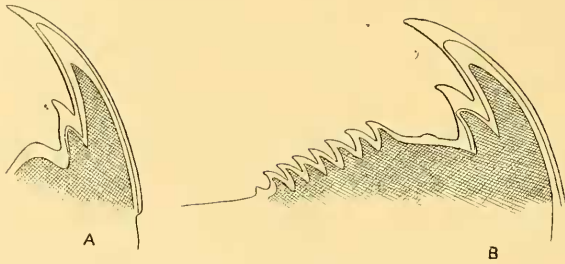


FIG. 1.—*A* outer, *B* inner blade of jaw of *P. Sedgwicki*.¹
(After Sedgwick.)

3. Legs with four to seven spinous pads (Fig. 2).

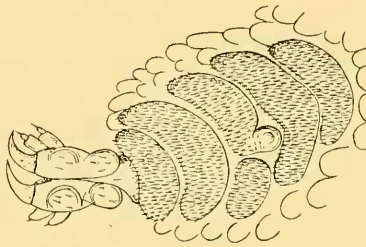


FIG. 2.—*P. ecuadorensis* Bouv., female. Ventral view of fourth leg, showing the pads, the position of the nephridial opening, and the pedal papillæ. (After Bouvier.)

4. Nephridial openings of legs four and five on the proximal side of the fourth pad either attached to it or separate from it.

5. Feet with three (Caribbean species), or from four to seven (Andean, Fig. 2), distal papillæ.

6. The genital opening is between the legs of the penultimate pair.

7. Oviduct is provided with a receptaculum seminis, which contains spermatozoa, and has two ducts (Fig. 3).

¹ This is the Venezuelan species referred to in the footnote on p. 395.

8. Oviduct is provided with a receptaculum ovarum (Fig. 3).

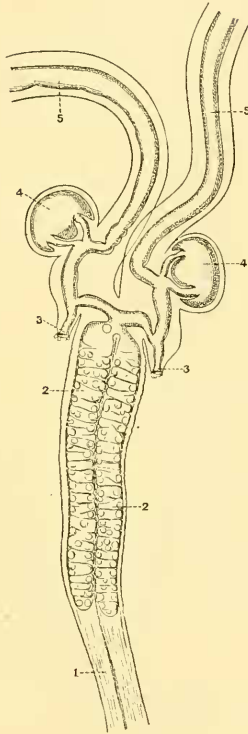


FIG. 3.—Female generative organs of *P. trinidadensis*. (After Gaffron.) 1. Funiculus. 2. Ovary. 3. Duct or funnel of the receptaculum ovarum; the latter is not shown. 4. Receptaculum seminis with its two ducts. 5. Anterior end of uterus.

9. The oviducts are united at the ovary (Fig. 3).

10. The ovary is endogenous, i. e. the wall of the ovarian tube is thick, and the ova lie in the thickness of the epithelium (Fig. 4). This character was first called attention to by Willey (1898), who contrasts it with the condition found in *Capo-* and *Austro-Peripatus*, etc., in which the wall of the ovary is thin, and the maturing ova do not retain their

epithelial position, but cause the ovary to project in the form of follicles into the body-cavity (exogenous ovary, Fig. 4).

11. Ova minute, $\cdot 04$ mm. in diameter.

12. Embryo provided in its young stages with a trophic vesicle, within which it lies.

13. Uterine embryos of all ages and born all the year round.

14. Unpaired part of vas deferens long and complicated.

FIG. 4.

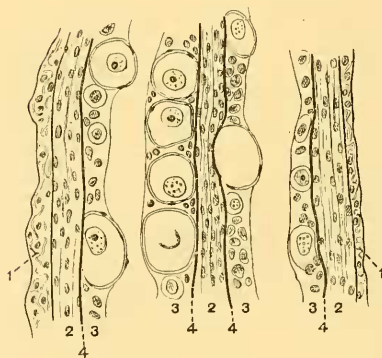


FIG. 5.

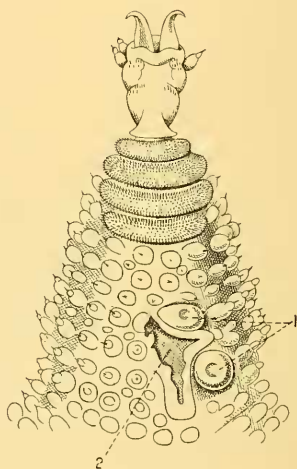


FIG. 4.—Horizontal section through the ovarian tubes of *P. trinidadensis*. (After Gaffron.) 1. Peritoneum traversed by tracheæ. 2. Tunica muscularis. 3. Germinal epithelium. 4. Tunica propria.

FIG. 5.—Ventral view of one of the posterior legs of a male *P. Sedgwicki*¹ Bouv. (After Sedgwick.) 1. Papillæ of crural glands. 2. Coxal organ. There are two papillæ on the anterior side of the distal part of the foot and one on the posterior.

15. Spermatophores elongated and with a thick case; often only one is present.

16. Skin pigment brownish, extracted by alcohol. The pigment appears to be dissolved out by the alcohol, which becomes tinged with brown, but the colour soon fades.

¹ See footnote on p. 384.

17. Legs with well-developed coxal organs (Fig. 5). There are furrows on the ventral side of the bases of the legs provided with tumid lips and lined by a smooth, non-tuberculate epithelium.

18. Crural glands in many legs in the males opening on papillæ (Fig. 5).

19. The accessory glands of the male open separately at the sides of the anus.



FIG. 6.—Fourth leg of a female *P. Tholloni*, ventral view.
(After Bouvier.)

CONGO-PERIPATUS.—A single species, *P. Tholloni*, has been described by M. Bouvier from the French Congo. They were found among leaves on vegetable humus round the trunk of an *Elaeis guineensis* at Ngômô in Ogôoné. Only a few specimens have been found, and it is possible that other species will be discovered. It is quite distinct from the Capo-Peripatus, and must be regarded as constituting a distinct type. Its characters are as follows:

1. Number of legs (twenty-four to twenty-seven pairs) is variable in the same species.

2. Inner jaw with a diastema and a saw of denticles.

3. Legs with three spinous pads (Fig. 6).
4. Nephridial openings of legs four and five on the proximal side of the third pad (Fig. 6) and attached to it.
5. Feet with three distal papillæ (two in front and one behind).
6. Genital openings between the legs of the penultimate pair.
7. Oviduct is provided with a receptaculum seminis. It is not known whether it contains spermatozoa or has two ducts.
8. There is a receptaculum ovarum smaller than in *Neo-Peripatus*.
9. The oviducts and ovaries are entirely separate from one another.
10. It is not clear from those writings of Bouvier which are accessible to me (1907), whether the ovary is endogenous or exogenous. I gather that it is endogenous.
11. Size of ripe ova not determined, not less than .06 mm. (Bouvier, '07, p. 345).
12. Young embryonic stages not known.
13. Uterine embryos differ much in age. Those near the uterine opening collect into a large uterine dilatation.
14. Unpaired part of vas deferens of great length.
15. Spermatophores unknown.
16. Skin pigment brownish, extracted by alcohol.
17. Legs with well-developed coxal organs.
18. Crural glands in the two pairs of pre-genital legs in male (two pairs on each leg) opening on papillæ.
19. The accessory glands of the male open in front of the anus in a common furrow.

Bouvier, in commenting on this species ('07, p. 336) deprecates giving it a generic name on the ground that we do not know what the future discoveries in equatorial Africa have in store for us; precisely the same reason, be it observed, that actuated me in declining to name my four groups. It would be interesting to know M. Bouvier's reasons for adopting generic rank for those species while declining it for his own.

This species undoubtedly has, at first sight, a strong look of *Neo-Peripatus*, but the characters 3 + 5, 9, and 13, in which it appears to be unique, are sufficient to separate it; and it must not be forgotten that we are ignorant of the nature of its egg and early development. In 18 and 19 it seems to resemble only *Eo-Peripatus*.

EO-PERIPATUS.—Four species are known in Malaya, three from the States of Jalor and Kelantan in the Peninsula (Evans), and one from Sumatra (Horst, Evans). The characters are as follows:

1. Number of legs (23—25 pairs) usually variable in the same species.

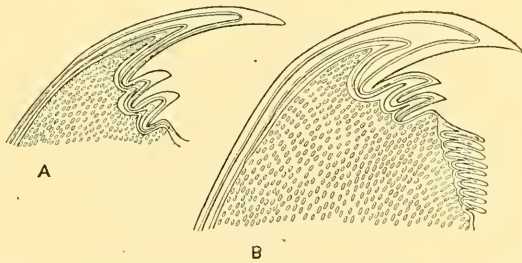


FIG. 7.—*A* outer, *B* inner jaw of *P. Weldoni*. (After Evans.)

2. Inner jaw with a diastema and a saw of denticles (Fig. 7).

3. Legs with four spinous pads.

4. Nephridial openings of legs four and five either in the proximal pad (*Weldoni*, *Sumatranus*) or proximal to it (*Horsti*, fig. 8).

5. Feet with two distal papillæ, one on the anterior and one on the posterior side.

6. Genital opening between the legs of the penultimate pair.

7. Receptacula seminis, with two ducts opening into the oviducts, are present.

8. Receptacula ovarum are present opening into the oviducts close to the ovary; no eggs have been found in them.

9. The oviducts are united at the ovary.

9a. The ovaries are completely fused, and contain one spacious cavity, and are attached to the floor of the pericardium by an extensive surface.

10. The ovary is exogenous, i. e. it is studded with follicles in which the maturing ova lie.

11. The ova are large and heavily charged with food-yolk. They measure about 1 mm. in their longest diameter.

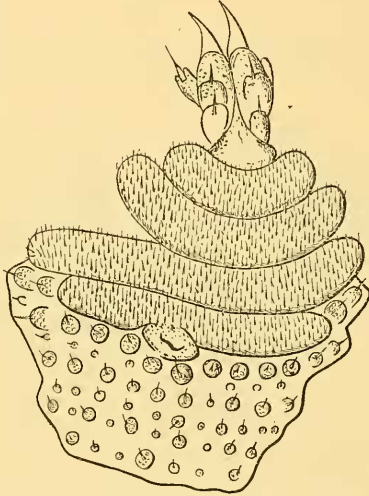


FIG. 8.—Ventral view of fifth leg of female *P. Horsti*.
(After Bouvier.)

12. Embryo without a trophic vesicle.

13. Uterine embryos of all ages.

14. Unpaired part of vas deferens nearly as long as that of *Neo-Peripatus*.

15. A single long spermatophore without a horny coat, but with a horny cap at its front end.

16. Skin pigment brownish; it is not stated that it is affected by alcohol.

17. Legs with well-developed coxal organs.

18. Crural glands in the male in the two pairs of legs preceding the genital opening; there are two pairs in each leg; they open into the groove of the coxal organ, and are without papillæ.

19. The accessory glands of the male open between the legs of the last pair by a common opening.

This is an exceedingly interesting group of species, for it shows, together with several peculiar features, viz. 3 + 4, 5, 9a, an important character only found elsewhere in Austro-Peripatus, viz. 11; and in the form of its jaws, in the number of its spinous pads, the position of the genital opening, the presence of a receptacula ovarum, it approximates markedly to Neo-Peripatus. But it is removed from Neo-Peripatus by its exogenous ovary, as well as by its large ova. It appears to hold 14 and 15 in common with Neo-, Congo-, and Austro-Peripatus. On the whole this group of species is as distinct as any, and is especially interesting as showing a mingling of characters which are found elsewhere only in Neo-Peripatus or in Austro-Peripatus. On the other hand it is worthy of remark that it shows nothing in exclusive community with Capo-Peripatus.

MELANO-PERIPATUS.—In 1897 Peripatus was discovered by Dr. A. Willey in New Britain. He wrote a full description of its anatomy and development, and named it *P. novæ-britanniæ*. Its characters are as follows:

1. The number of legs (22—24 pairs) is variable in the species.

2. The outer jaw is without a minor tooth, and the inner jaw has no diastema or saw.

3. Legs with three spinous pads.

4. Nephridial opening of legs 4 and 5 are on the proximal pad.

5. Feet with three distal papillæ, one of which is anterior, one dorsal sometimes inclined to the anterior side, and one posterior (Fig. 9).

6. Genital opening subterminal behind the legs of the last pair.
7. Oviduct with a receptaculum seminis with two ducts.
8. Receptacula ovarum absent.
9. The oviducts are united at the ovary.
10. The ovary is exogenous.
11. Ova of medium size (.1 mm. in longest diameter) with little yolk.

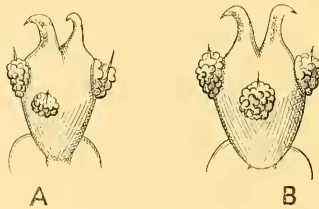


FIG. 9.—Dorsal views of feet of *P. novæ-britanniæ*, showing the primary papillæ. In *a* the dorsal papilla is inclined to the anterior papilla; in *b* it is median. (After Willey.)

12. Embryo in its young stages provided with a large dorsal appendage, consisting of ectoderm and endoderm, and called by Willey the trophic vesicle.
13. Uterine embryos of all ages in the same uterus.
14. Unpaired part of vas deferens, very short, almost obsolete.
15. Spermatophores absent.
16. Skin-pigment black, apparently not affected by spirit.
17. Legs without well-developed coxal organs.
18. Crural glands absent.
19. Accessory glands of the male open medianly and dorsally near the hind one.

This species, which we should expect from its locality to resemble *Austro-Peripatus*, presents seven peculiar features, 6, 11, 12, 14, 15, 19, of which 6, 11, 14, and 19 are important morphologically. By having a receptaculum seminis with two ducts and no receptacula ovarum it presents a combination of characters found elsewhere only in

Austro-Peripatus. The skin-pigment appears to be peculiar, but in not being affected by spirit it approaches *Capo-* and *Austro-Peripatus*; and the same may be said about the absence of well-developed coxal organs, and the form of the jaws. Its affinity would appear to be closer to *Austro-* and *Capo-Peripatus* than to *Neo-Peripatus*, but it differs from *Austro-Peripatus* in the variability of its leg number (1) and in its ovum. On the other hand it has no crural glands, a feature which is found elsewhere only in *Austro-Peripatus*. The form of its ovum (11) and its trophic vesicle (12), though peculiar characters, are nearer the corresponding structures in *Capo-Peripatus*, as also is the structure of its vas deferens (14). On account of the number of its peculiar features we have no hesitation in establishing it as a distinct group, but we think it is considerably nearer to *Capo-Peripatus* than to *Austro-Peripatus*, from which it is distinguished by the very important characters of its ovum as well as by its leg-number.

CAPO-PERIPATUS.—*Peripatus* is found in Natal and Cape Colony. It is represented by seven well-established species (Purcell, 1899), which exhibit the following characters:

1. The number of legs (16—25 pairs) is variable when the number of pregenital legs exceeds 19 pairs.
2. Outer jaw with one minor tooth; inner jaw without diastema or saw.
3. Legs with three spinous pads.
4. Nephridial openings of legs 4 and 5 on the proximal pad.
5. Feet with three distal papillæ, two anterior and one posterior, except in one species, *cinctipes*, in which one of the anterior papillæ is dorsal.
- 5*a*. Feet with two papillæ at the base of the foot (Fig. 10), except in one species, *cinctipes*.
6. Genital opening between the legs of the last pair which

show a tendency to reduction, and are sometimes obsolete (*P. capensis*).

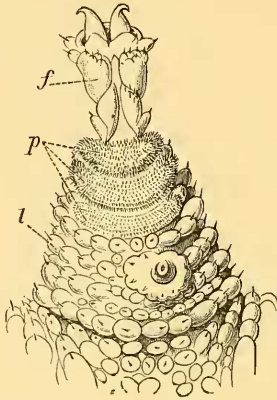


FIG. 10.—Ventral view of last leg of a male of *P. capensis*. (After Sedgwick.) *f*. Foot. *l*. Leg. *p*. Spiniferous pads. The papillæ on the proximal part of this leg is characteristic of the male of this species.

7. Receptaculum seminis absent, except in *cinctipes*, in which there is said to be a minute trace of one. It is, however, caused by a loop of the epithelial tube (Fig. 11).

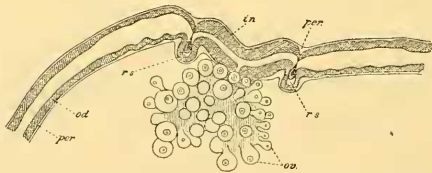


FIG. 11.—Ovary and oviduct of *P. cinctipes*, showing the minute receptaculum seminis, *rs*. (After Purcell.) *ca*. Thick wall of infundibular part of the oviduct. *od*. Thinner wall of oviduct. *ova*. *per*. Peritoneum and muscles of oviduct.

8. Receptacula ovarum absent.
9. Oviducts united at ovary (Fig. 11).
10. The ovary is exogenous.
11. Ova comparatively large, with but little yolk (·56 mm.

in greatest diameter in *P. capensis*, in *P. Balfouri* .4 mm.; in *P. cinctipes* it is smaller, probably about .2 mm., but its length is not given by Purcell).

12. Embryos usually without trophic vesicles, but Bouvier states that there is a tendency to a dorsal trophic vesicle like that of *Melano-Peripatus* in two species (*P. Sedgwicki*¹ and *Moseleyi*).

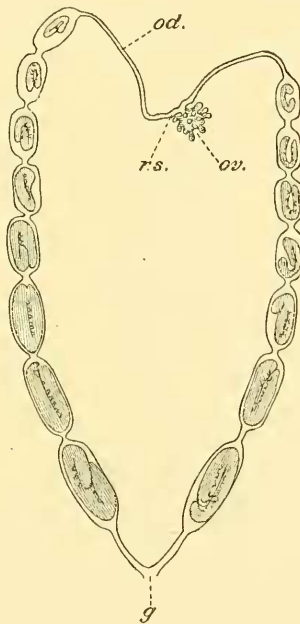


FIG. 12.—Female generative organs of *P. cinctipes*. (After Purcell.) *ov.* Ovary. *rs.* Receptaculum seminis. *od.* Oviduct. *g.* Genital opening.

13. Uterine embryos of nearly the same age. They differ most in *P. cinctipes* (Fig. 12), in which, however, the difference is not very great.

14. Unpaired part of vas deferens short.

¹ So named by Purcell. Bouvier has applied the same name to a species of *Neo-Peripatus* found in Venezuela (this footnote is referred to on p. 384).

15. Spermatophores small, oval, with a thin coat.

16. Skin pigment blue, green, or black, not affected by spirit. A certain amount of brown or orange is often present, especially on the ventral surface.

17. Coxal organs variable; usually not well developed. In *P. Sedgwicki* and *Moseleyi* they are moderately developed, and in *P. cinctipes* well developed.

18. Crural glands present in most legs of both sexes, except possibly in *P. cinctipes*, in which they have not been found by Purcell in the females.

19. The accessory glands of the male open into the terminal part of the vas deferens, except in *P. cinctipes*, in which they open separately between the anus and genital opening.

The South African group of species presents a greater variation of structure in the selected characters than any of the other groups.

The variable characters are:—(1) The legs on each side of the genital opening, No. 6. (2) The coxal organs, No. 17. (3) The size of the ova, No. 11. (4) The presence of a trophic vesicle. These vary throughout the group. In addition to these we find in *P. cinctipes* variability in the pedal papillæ, a variability similar to that found in the same character in *Neo-Peripatus*. Moreover, this species is said to possess a minute receptaculum seminis found in no other species of the group, and a variation in No. 19. *P. cinctipes*, on account of its peculiarity in these three characters, Nos. 5, 7, 19, has been established by Purcell as a special genus, *Opisthopatus*, which has been accepted by Bouvier. I find myself quite unable to admit that the characters mentioned are sufficient to justify the separation of *P. cinctipes* from the rest of the group. The differences are not greater than those which separate the Andean from the Caribbean species of *Neo-Peripatus*, and no one has proposed to separate these from one another.

The assemblage of characters which leads me to assert the homogeneity and distinctness of the group are those numbered

2, 3, 4, 6, 7, 11, 12, 13, 14, 15, 16, 17, and 18. Of these the most important, and not found in any other group, are 7, 11, and 13 (the receptaculum seminis of *P. cinctipes* is so very small and simple that it hardly affects the point). But, although I assert the distinctness of the group, it must be confessed that it approaches *Melano-Peripatus* more closely, perhaps, than do any other two groups of species, not even excepting *Neo-Peripatus* and *Congo-Peripatus*. This is especially shown by the form of the jaws and the nature of the ovum, No. 11; through the species *cinctipes* in the arrangement of the distal pedal papillæ, No. 5; through the species *Capensis* in the absence of genital legs, No. 6; through the species *Sedgwicki* and *Moseleyi* in the tendency towards the presence of a trophic vesicle, No. 12; through most of the Cape species in the absence of well developed coxal organs, No. 17; and in the shortness of the unpaired part of the vas deferens. But the distinctness of *Melano-Peripatus* cannot be impugned, having regard to its characters 6, 7, 11, 12, 14, 18, and 19.

AUSTRO-PERIPATUS.—*Peripatus* is known from both Eastern and Western Australia, from Tasmania and from New Zealand. It is interesting to note that it has not so far been found in New Guinea. All the species known, of which there are eight, belong to the group *Austro-Peripatus* (*Peripatoides* of recent authors). The characters are as follows:

1. The number of legs (14 to 16 pairs) is constant in the same species.

2. The outer jaw is either without minor teeth or with one or more minor teeth; the inner jaw is without a diastema or a saw.

3. The legs have three spinous pads.

4. Nephridial openings of legs 4 and 5 on the proximal pad.

5. Feet with three distal papillæ (one anterior, one dorsal,

and one posterior), except in *P. suteri*, in which there may be three or four.

6. The genital opening is between the legs of the last pair, which are normally developed.

7. The oviduct is provided with a receptaculum seminis with two ducts.

8. Receptacula ovarum absent.

9. The oviducts are united at the ovary.

10. The ovary is exogenous.

11. The ova are very large (from 1.5 to 2 mm. in longest diameter) and heavily yolked.

11a. In some species the opening of the vagina is at the end of a long ovipositor (*viridimaculatus*, *insignis*, *Leuckarti*, *oviparus*) and the eggs are probably laid. *P. oviparus* and *viridimaculatus* are certainly oviparous, and their eggs have sculptured shells.

12. Nothing corresponding to a trophic vesicle.

13. Uterine embryos of markedly different ages or of about the same age.

14. Unpaired part of vas deferens long and complicated.

15. Spermatophore single and elongated, with a thick case.

16. Skin pigment mainly black, blue, green, or brown, unaffected or but slightly affected by spirit.

17. Legs without well-developed coxal organs.

18. Crural glands present in some species (*Suteri*, *novæ-zealandiæ*), absent in others. When present, in the males only.

19. Accessory glands of the male opening separately between the anus and genital opening; in some species the openings are far apart, in others (*P. Leuckarti*) close together between the genital opening and the anus.

On the whole, this group of species, which ranges over the whole of Australia, Tasmania, and New Zealand, presents but little variation. There is a little variation in the outer blade of the jaw, in the pedal papillæ, in the relative ages of embryos in the same uterus, and in the crural glands. Also in three of the species the oviduct opens at the end of a

papilla—the ovipositor. This character is associated in two of the three species (and possibly in the third) with an oviparous habit and a sculptured egg-shell. It has been proposed to segregate these three species in a special genus, *Ooperipatus*, but, having regard to the fact that all *Austro-Peripatus* approach the oviparous condition, some even abnormally extruding eggs, this character of oviparity cannot be regarded as sufficiently important to confer generic rank. This view is still further emphasised by Bouvier, who points out that to adopt it will create confusion in the arrangement of the other species of the group, the oviparous forms not being monophyletic.

The only character absolutely peculiar to the group is No. 1. The other characters are distributed fairly impartially in most of the other great groups. Thus No. 6 is found in some of the *Capo-Peripatus* and then only imperfectly, and the colour also takes after that of the South African forms. The presence of well-developed receptacula seminis without receptaculum ovorum is found elsewhere only in *Melano-Peripatus*; and the absence of well-developed coxal organs and the arrangement of the pedal papillæ occur again only in *Melano-Peripatus*, *Chilio-Peripatus*, and some species of *Capo-Peripatus*. The character and size of the ova are found elsewhere only in *Eo-Peripatus*, and the length of the unpaired part of the vas deferens and nature of the spermatophore only in *Neo-*, *Congo-*, and *Eo-Peripatus*. From this summary it is doubtful, to say the least of it, if *Austro-Peripatus* shows any special affinity to any other group of species. At first sight one might be inclined to assert an approach to *Melano-* and *Capo-Peripatus*, but having regard to the important characters Nos. 1, 11, and 14 this view can hardly be maintained.

CHILIO-PERIPATUS.—One species of *Peripatus* has for long been known from Chili, but it is only comparatively recently that its characters have been made known to us by Bouvier. It occurs far to the south of any *Neo-Peripatus*,

and is entirely distinct from that group.¹ Its characters are as follows :

1. Number of legs variable (19 to 21) in the same species.
2. Outer jaw with two minor teeth, inner jaw without a diastema and saw.
3. Legs with three spinous pads.
4. Nephridial opening of legs 4 and 5 on the proximal pad.
5. Feet with three distal papillæ, one of which is dorsal.
6. Genital opening between the legs of the last pair, which are reduced in size.
7. Receptaculum seminis, if present, very much reduced, without double duct.
8. Receptaculum ovarum absent.
9. Oviducts united at the ovary.
10. The ovary is endogenous.
11. Ova small (.07 mm.), but not so small as in *Neo-Peripatus*.
12. The embryos are without a trophic vesicle.
13. Uterine embryos of markedly different ages, but arranged in groups of three, the embryos of each group being of the same age (Fig. 13).
14. Unpaired part of vas deferens short as in *Capo-Peripatus*.
- 14a. A part of the vas deferens on each side is coiled into a close spiral.
15. The spermatophores are multiple, small, and cylindrical, without a specially thick case.
16. Green or black, with reddish patches, but little affected by spirit.
17. Without well-developed coxal organs.
18. Crural glands unknown in either sex.
19. The openings of the accessory glands of the male are unknown.

¹ It is beyond the scope of this paper to deal with the geographical significance of the occurrence of a distinct specific group of *Peripatus* on this part of the South American Continent.

I think that there can be little doubt that an impartial consideration will assign to this species the rank of an independent group. Though it approaches by its colour, and by the characters of its jaws, legs, and feet, Capo-, Austro-, and Melano-Peripatus; it differs absolutely from those groups by its endogenous ovary, found elsewhere only in Neo-Peripatus, by the small size of its ova, and by the important characters 13 and 14a. By its feet it is more

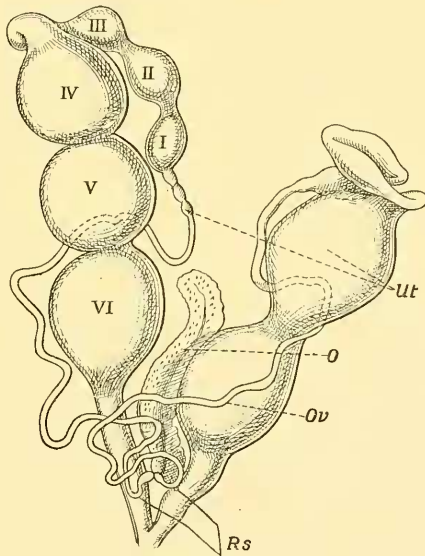


FIG. 13.—Ovary and gravid uterus of *P. Blainvillei*. (After Bouvier.) *Rs*. Supposed receptaculum seminis. *O*. Ovary. *Ov*. Oviduct. *Ut*. Uterus. I, II, III. Embryos of one group. IV, V, VI. Embryos of the next group.

especially approached to Austro-Peripatus, by the unpaired part of its vas deferens to Capo-Peripatus. It is undoubtedly more closely allied to the Austro- and Capo-Peripatus than to the Neo-Peripatus, but its ova approach those of Neo-Peripatus more closely than do those of any other form, and it has an endogenous ovary. We get, therefore, here again the same intermingling of characters of

different species-groups that we have before met with in each of the species-groups, together with a certain number of entirely peculiar features. In assigning to Chilio-Peripatus (*Peripatus Blainvillei*) independent rank I am at issue with Bouvier. He associates it with the South African species *Peripatus cinctipes* in Purcell's genus *Opisthopatus*. He bases this association on the character of the ovum (considerably smaller than that of *cinctipes*), on the arrangement of the distal pedal papillæ (found also in Melano- and Austro-*Peripatus*), and on the presence of a very minute receptaculum seminis. But, as stated above, the ovum is much smaller than that of *cinctipes*, approaching more closely to that of Neo-*Peripatus*, and it is doubtful if the very small dilatation called receptaculum seminis is really homologous with that structure in other species. I am quite unable, therefore, to admit the association of *Blainvillei* with *cinctipes* any more than I can admit the genus *Opisthopatus* itself. It seems to me clear that Bouvier, in placing it with *cinctipes*, has been actuated largely by his hypothetical views as to the place of origin and evolution of the genus. These views, based, as such views generally are, upon à priori considerations as to the primitiveness of certain characters and the more recent origin of others, have no real validity, and tend to obscure the important issues, upon which the facts of classification and distribution can help to throw light. The futility of this method of speculation is further emphasised by the fact that the results obtained by it vary directly according to the theoretical bias of the author. Bouvier, who regards the presence of the maximum number of structures (1907, p. 70), whether legs, segments, spinous pads, etc., as a sign of primitiveness, places Neo-*Peripatus* nearest a supposed original form, whereas Evans (1901*a*, p. 525), who considers a large and heavily yolked egg as an antique character, regards as the most primitive group Eo-*Peripatus*, which by Bouvier is regarded as the most advanced. Such diverse results may well inspire doubt as to the value of the method employed.

What, then, are the important lessons which the distribution of the species of the genus *Peripatus* teach us. They are, I take it, two in number:—(1) The geographical groups of species are natural zoological groups, the members of which are more closely related to each other than to those of the other groups. (2) The distinguishing specific characters are distributed in an entirely haphazard manner in the different specific groups, so that it is quite impossible to show the phylogenetic affinities of the specific groups by any tree-like arrangements.

On the first of these two points I have already said enough; enough, I hope, to convince all candid minds of its truth. On the second it is necessary to dwell a little longer. Let me take the case of *Eo-Peripatus*, which is associated by Bouvier with *Neo-Peripatus* in his family *Peripatidæ*. It borrows, so to speak, its large and yolked ovum from *Austro-Peripatus*; the number of its spinous pads from *Neo-Peripatus*; its inner jaw, the position of its genital opening, its receptacula ovarum, its skin pigment from *Neo-* and *Congo-Peripatus*; its receptacula seminis, the length of the unpaired part of the vas deferens, the form of the spermatophore from *Congo*, *Neo-*, and *Austro-Peripatus*; the opening of the accessory glands of the male from *Congo-Peripatus*; and lastly, the well-developed coxal organs from *Congo-Neo-*, and some of the *Capo-Peripatus*. And, in addition to this mingling of characters of other groups, it possesses the following peculiar features found in no other species: the position of the nephridial opening of legs 4 and 5, the number of distal pedal papillæ, and the complete fusion of the two ovaries (No. 9a).

Or again, let us take *Congo-Peripatus*, which is associated by Bouvier in the same genus as *Neo-Peripatus*. It has only borrowed one character exclusively from *Neo-Peripatus*, viz. the position of the nephridial openings on legs 4 and 5. It has borrowed the opening of its accessory glands and crural glands from *Eo-Peripatus*; its inner jaw, the position of its genital opening, its receptacula ovarum, its skin pigment from

Neo- and Eo-Peripatus; its receptaculum seminis, the length of the unpaired part of its vas deferens from Neo-, Eo-, and Austro-Peripatus; its distal pedal papillæ from Capo-, Austro-, and Neo-Peripatus; its spinous pads from Capo-, Melano-, and Austro-Peripatus; its well developed coxal organs from Eo-, Neo-, and some Capo-Peripatus. Lastly, in the complete separation of its female generative tracts (No. 9), and the peculiar method of housing its uterine embryos (No. 13), it stands apart from all other species. Looked at in this comprehensive way, which is the only fair way, there seems to be nothing to be said for placing *P. Tholloni* with Neo-Peripatus.

Lastly, let us look at *Peripatus cinctipes*, which occurs geographically with Capo-Peripatus, and consider whether it ought to be separated from this group and placed in a special genus. The series of forms found in South Africa admittedly present a greater variation in structure than any other group. Some of these variations are found throughout the group, others are confined to *P. cinctipes*. It will only be necessary for us to consider the latter. These are (1) a difference in the number and position of the pedal papillæ, (2) the presence of a minute receptaculum seminis, (3) a difference in the method of opening of the accessory glands of the male. With regard to (1) the distal papillæ vary from the type less than do those of the Andean species of Neo-Peripatus amongst one another, and a very similar variation is presented by different individuals of the single species of Melano-Peripatus. But this is not the only difference from the type; the basal pedal papillæ, so characteristic of the Capo-Peripatus in general, are absent. This, though important, is not sufficient to justify the establishment of the genus *Opisthopatus*. Nor are the other two; for the receptaculum seminis is different to the usual form of that organ, and so small that its homology is doubtful, and it may easily have been overlooked in other species, and the difference in the openings of the accessory glands is paralleled in Austro-Peripatus. The absence of the basal pedal papillæ

not being sufficient in itself to justify the establishment of a genus (it is quite possible that further research on *Capo-Peripatus* may disclose other species in which they are absent), I am led to reject the genus *Opisthopatus*.

It would be tedious to continue this detailed examination. The reader can easily do it for himself, and if he does so he will, I think, convince himself of the truth of my two main contentions: (1) that the geographical groups are natural groups, (2) that the distinguishing specific characters are distributed in an entirely haphazard manner amongst them. The conclusions which I draw from these facts (as I venture to regard them) are two in number. First I infer that the present species of *Peripatus* are derived from a single widely ranging species roughly extending within the limits of the present distribution; and secondly, that this species was highly variable, including within the range of its variation all the different characters at present presented by the whole genus.

Of these two inferences the first will generally be conceded to have some possibility of truth. The second is not so obvious. It is one which I have long held as a principle which explains many difficulties and anomalies in classification. I base it on the significant intermixture of characters, which is presented not only by the genus *Peripatus* but by many groups of the animal kingdom; an intermixture of characters which on the ordinary views of the theory of evolution are quite incompatible with one another; an intermixture of characters, which, by all the canons of ordinary morphological criticism, are primitive, with characters which are specialised. I have called attention to the phenomenon more than once in my work on 'Zoology.' For instance, in the second volume, p. 618, in dealing with the relationship of the main groups of the Carnivora I say, "What we have here is merely an example of the principle to which we have so often before called attention in this work, that the more closely any given group of animals is studied, the more complex are the mutual relations between its different mem-

bers found to be," and I refer the reader to the case of the Nudibranchiata in vol. i, p. 410, which prominently illustrates the same principle. I might also refer to the case of fishes (*Chimæra* and the *Dipnoi*) as remarkable instances of the same phenomenon.

The case imagined for *Peripatus* is very similar to that of the human race, which consists of an almost continuous, interbreeding and variable species. The Australian may be said to bear the same relation to the negro—lacking the frizzy hair, as *Eo-Peripatus* does to *Neo-Peripatus*—lacking the small ovum.

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